EGGS OF RIODINIDAE

John C. Downey

Biology Department, University of Northern Iowa, Cedar Falls, Iowa 50613

AND

Arthur C. Allyn

Allyn Museum of Entomology, 3701 Bay Shore Road,
Sarasota, Florida 33580

ABSTRACT. Descriptions and SEM photographs of the eggs of 13 species of Riodinidae are given together with morphological and taxonomic viewpoints of their comparison to eggs of the Lycaenidae.

In our ultrastructural studies of lycaenid eggs (Downey & Allyn, 1980), we have become aware of the lack of comparative details on the egg state of most families of Lepidoptera. Through the kindness of Roy and Connie Kendall, we were able to examine the chorionic structure of riodinids of 13 species representing six genera with the scanning electron microscope (SEM). Most of the life histories of these species have yet to be described. We are unaware of SEM studies on this interesting family. These observations and preliminary notes may be of general interest and may stimulate additional studies. We dedicate this effort to the memory of our friend and colleague, Harry K. Clench, who was enthusiastic about new data on this family and its relationship to the Lycaenidae.

Materials and Methods

All eggs were laid by females (rather than extracted) and were collected and stored in alcohol. Our studies indicate that dried eggs dispatched by cyanide or freezing may be slightly superior to alcohol-stored eggs for SEM examination. The latter are perfectly adequate for SEM work, though they may have lipids and other alcohol extracted materials (see Fig. 19) adhering to the surface, and might best be cleaned with solvent, or sonically cleaned, prior to coating. Freshly collected eggs stored in alcohol also have a tendency to collapse, whereas eggs which have chorions exposed to the air for a few hours seem to retain their shape. Specimens were mounted on JEOL holders by means of double-sided tape edged with a conductive lacquer adhesive prior to coating. They were coated with 40/60 gold-palladium in a Varian V-10 vacuum coater and studied with a JSM-U3 instrument. Results are presented with both descriptions and photographs.

Results

All eggs examined are of the upright type, with the micropyle on the "top" surface opposite the flattened "bottom" surface, which is affixed to the substrate. Although the shapes and sizes of the eggs vary, the micropylar axis (height) is always shorter than the transverse axis (diameter). Most eggs are round when viewed from above, though elevated ribs may disrupt the circumference silhouette. The profile or side view varies from partially flattened, to turban and dome shape in different species. The micropyle is centered on the upper surface and surrounded by a rosette of petal-shaped cells which are outlined by delicate lines. The remaining surface of the chorion is variously sculptured with somewhat defined elevations which appear to impart a species-specific character to the egg. Aeropyles, tiny openings extending into or through the meshwork of the outer chorion, may or may not be visible, and may be located on prominences or (as pores) on relatively flat areas of the chorionic surface. Descriptions of eggs of the individual species follow.

Calephelis rawsoni McAlpine
Figs. 8, 17, 18
d(diameter). 0.62 mm; h(height). 0.28 mm

Egg rounded in dorsal view, though the vertical elevated ridges and protuberances cause irregularities in the circumference shape; in profile flattened on the micropylar surface and angled both at the shoulder, and (less marked) toward the bottom surface; with a marked annulus surrounding the micropylar area, from which 15 ribs radiate outward like spokes in a wheel; the ribs abruptly arch upward as they abut the collar or annulus (Fig. 17) in the manner of a flying buttress; the annulus is honeycombed with small depressions, which have irregular penta- or hexagonal walls, mostly on the upper and the mesial surface; the annulus appears non-porous in *rawsoni*, although many of the same honeycomb depressions in *perditalis* appear open and could serve as aeropyles; the lateral wall of the annulus drops off abruptly and is non-sculptured; the cells (areolae) between the radiating ribs have smooth, unsculptured bottoms, and are more regularly shaped; the second row of cells from the annulus are hexagonal and are set at about 45° from the top and sides of the egg; the ribs are almost perpendicular to the lower chorion; aeropyles are apparent on triangular-shaped prominences (Fig. 18) at the intersections of the ribs of the second row of cells; the third and fourth (bottom) row of cells from the annulus may have sharper prominences at the angle junctures but appear to lack aeropyles.

Micropyle, with four openings, is surrounded by rosette with seven to nine petals depressed into slightly convex surface; area between rosette and annulus smooth, with very faint shallow depressions of the size and appearance of fainter rosette cells.

Eggs from two localities in Texas show a minor degree of variability, particularly in the nature and degree of porosity in the annulus, and in the micropylar depressions. This may be individual rather than geographic variability. Specimens from Kerr Co., Texas, also have a small pore which is slightly larger than the aeropyle openings, which is located between the ribs and the lower chorion at the rib juncture sites beneath the aeropyles.
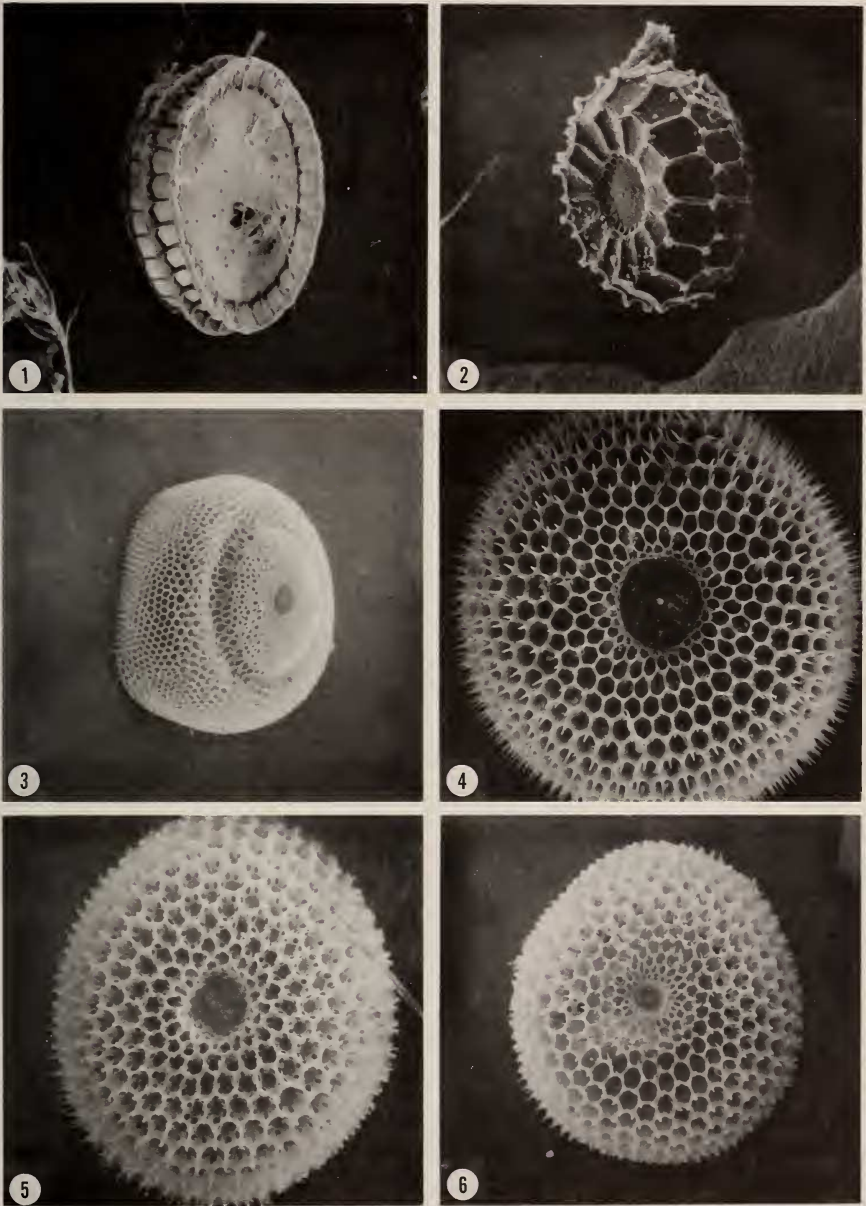
FIGS. 1–6.   SEM photos of the eggs of Riodinidae, 60×. **1,** *Lasaia sula penninsularis*; **2,** *Caria ino melicerta*; **3,** *Emesis emisea*; **4,** *E. mandana furor*; **5,** *E. tegula*; **6,** *E. tenedia*. Photographs reduced to 0.58 of original size.

Calephelis perditalis Barnes and McDunnough

Fig. 7
d. 0.60 mm; h. 0.30 mm

External appearance much like *rawsoni* except the collar, or annulus, is slightly smaller in *perditalis,* which also has larger and more open interstices in the honeycomb network; 14 spokes or radii of elevated ribs run from the annulus to the ribs of the second row of cells; 3 openings in micropyle.

In emerging from the egg the larva carves its way out by eating around the annulus, on the outside margin of this honeycomb collar.

Caria ino melicerta Schaus

Fig. 2
d. 0.58 mm; h. 0.30 mm

Chorionic structure similar to *Calephelis rawsoni* and *C. perditalis* except that it is lacking the heavy circum-micropylar collar or annulus; micropylar region slightly de- pressed, and around the margin of this region on the vertical face (between the micro- pylar plateau and the level of the surrounding cells) are 25 prominent aeropyles; 13 ribs radiate out from the aeropylar lips to join a chevron-shaped rib outlining the outer margins of the first row of cells; prominent tubercles protrude upward from rib junc- tions; these hillocks are irregularly shaped masses (like outpourings of lava from a volcanic eruption) and contain very small aeropyles, ¼ the size of the aeropyles in comparable positions in *rawsoni*; second row of cells slightly larger than in *Calephelis*, numbering 13; unique rib structure with either carina on some muri (circumpolar ten- dency), or central crenulations, running parallel to the rib axis (radiating & vertical rib tendency), giving the ribs the appearance of being composed of more than one parallel element; chorion of cells smooth and structureless.

Four holes in micropyle; micropylar rosette composed of 7 or 8 recessed petals which are very difficult to locate.

Lasaia sula penninsularis Clench

Figs. 1, 20
d. 0.62 mm; h. 0.28 mm

Circular in top view; unique lateral profile having a cup or bowl shape with lateral walls composed of two "rings" of cells with ribs between; lower or third row or ring of cells at about 30° from flattened bottom of egg, so this row is almost hidden in side view; lip of bowl composed of ribs between second row of cells (lateral in position) and first row of cells (dorsal in position) which are lying at 30° above the plane of the upper (micropylar) surface; circular ribs or muri between rows of cells are higher and thicker than vertical or cross ribbing between them, and they may or may not possess one to several carina or raised ridges along their surface; a few small aeropyles at rib junctions, irregularly placed; chorion of cells smooth and unstructured; upper mem- brane thin and overlaid with very delicate thin ribbing forming irregular hexagonal cells; micropyle with four holes in a small central depression; eight-petal micropylar rosette very difficult to see (Fig. 20) with petals outlined by delicate elevated ribs.

Compare Fig. 20 and 21 which show some of the difficulties of interpreting SEM photographs without the advantage of viewing the object from several directions. The rosette in Fig. 20 has petal outlines which appear to be troughs or depressions; actually they are elevated ribs which become apparent when the figure is viewed upside down. The petals of the rosette in Fig. 21 are outlined by negative depressions, linear inden- tations in the surface rather than ribs laid on top of the surface.

In Fig. 1, a portion of the thin, delicate upper membrane has been accidentally destroyed by the electron beam, and larval hairs may be noted in the opening. The first instar larva within was not coated, of course, and thus minor "charging" is reflected back through the thin chorionic "floor" of cells in the second and third row of cells,
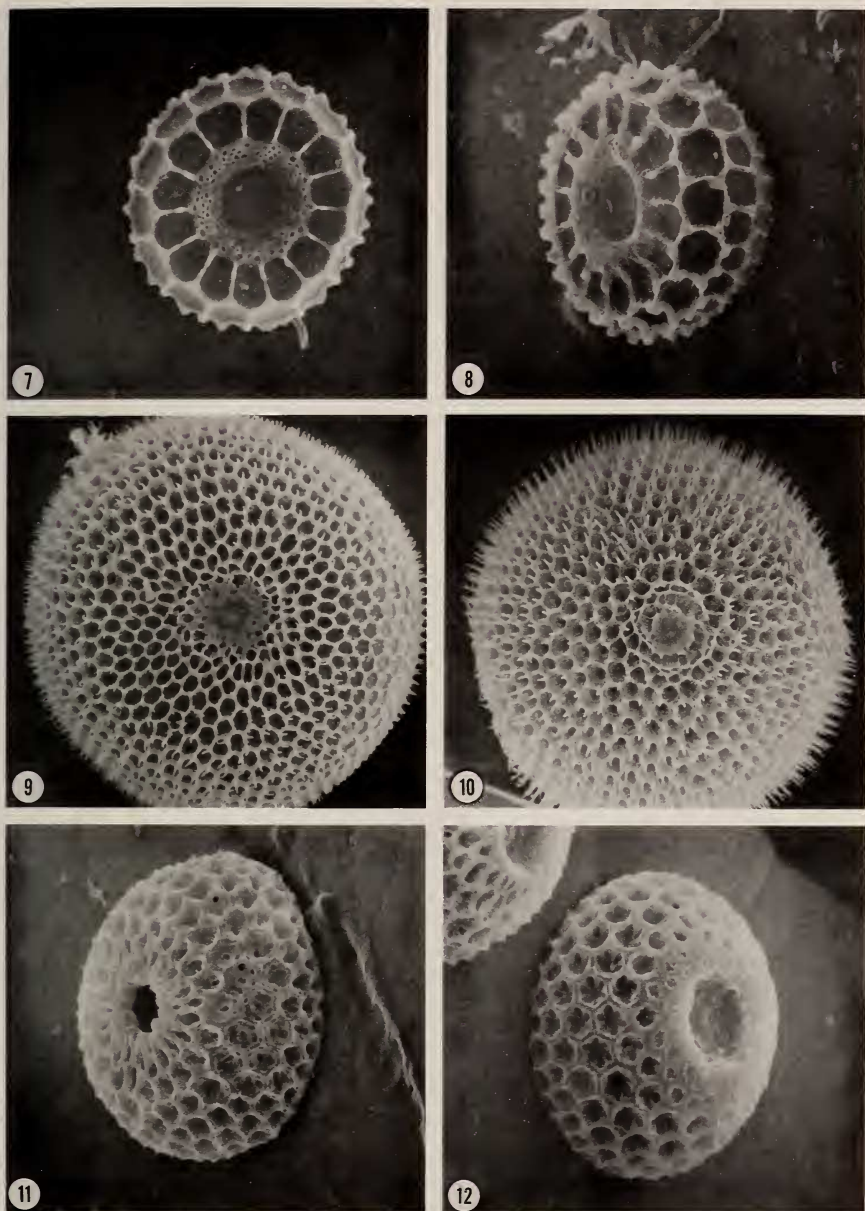
FIGS. 7–12. SEM photos of eggs of Riodinidae, 60×. **7**, *Calephelis perditalis*; **8**, *C. rawsoni*; **9**, *Apodemia mormo mejicana*; **10**, *A. chisosensis*; **11**, *A. palmeri*; **12**, *A. walkeri*. Photographs reduced to 0.58 of original size.

giving the entire egg a flying-saucer appearance (with "lights on" in the windows!). In life, the upper membrane is slightly convex, arching up somewhat from its junction with the first circular row of cells; the arch of the central micropylar "dome" is not as high as the outer edge (ribbing) of the first cell row, so that to the unaided eye the egg may appear strongly shouldered and flat on top.

Emesis emesia (Hewitson)
Figs. 3, 15, 21
d. 0.58 mm; h. 0.30 mm

Egg circular in dorsal view, turban-shaped in side view with the central half of the top surface seemingly depressed downward leaving a circular trough or indentation between apex and shoulder (Fig. 3); all but the micropylar area covered with marked hexagonal honeycomb network, the cells of which are larger (with hexagonal shape distorted) in the trough area; hexagonal cells more regular on sides and toward the bottom of the egg, but rounded on the elevated upper circum-micropylar area; ribs lining the cells in this transitional zone (between micropyle and trough) have dorsal crenulations (Fig. 15) giving them a "frothy" appearance; the roughened froth is arranged in smaller or larger circles atop the ribs, with smaller squares and irregular shaped openings placed at random as interstices between the circular cells; on the lateral surface, ribs are carinate, and describe almost perfect hexagons near their outer limits, while the cells they delimit near the bottoms of the ribs are nearly circular; the side walls of the ribs in this area have delicate vertical tracings which show a (micro-) pentagonal arrangement.

The micropyle consists of six large openings on a smooth surface (Fig. 21) which is quite outwardly convex; the rosette is barely discerned by negative outlines around the petals in an otherwise unstructured surface; the circular micropylar area is 0.08 mm in diameter and is slightly convex, bowed upward from the surrounding transition zone collar.

No aeropyles were noted leaving us to speculate whether or not the enlarged micropyles may serve in this capacity in this species.

Emesis mandana furor Butler and Druce
Fig. 4
d. 0.96 mm; h. 0.32 mm

Egg circular in horizontal section, dome shape in profile with the micropylar area (diameter 0.19 mm) slightly depressed into the apex of the dome; egg slightly wider, but not as high (in relation to its width) as other *Emesis* species; chorionic network highly reticulate, with hexagonal cells resembling a honeycomb covering all visible surfaces except the micropyle; the cells are arranged in a regular manner, appearing to be in linear or gently curving rows without, however, assuming repeatable patterns; cells largest at shoulders and upper sides, becoming smaller as they approach the micropylar region, where they are reduced to one-quarter size and become slightly distorted in shape as they "roll over" the lip of the slight vertical drop to the micropylar margin; spiny processes up to 0.04 mm long protrude from the rib intersections surrounding each cell so that the six cellular spines give a distinct echinoid appearance to the chorion; the spines are largest on the sides and shoulders, reduced on top, and are wanting near the apex; a carina runs along the crest of each rib and starts to run up the base of each spine before gradually disappearing; side cells have a convex shape, and a smooth surface, even though several folds or pleats run from the rib bases towards the center or lowest part of the cell.

Micropyle with eight holes arranged in circle; rosette difficult to detect; micropylar area of irregular or semi-undulating surface level with numerous pores of a size slightly larger than the micropyles.
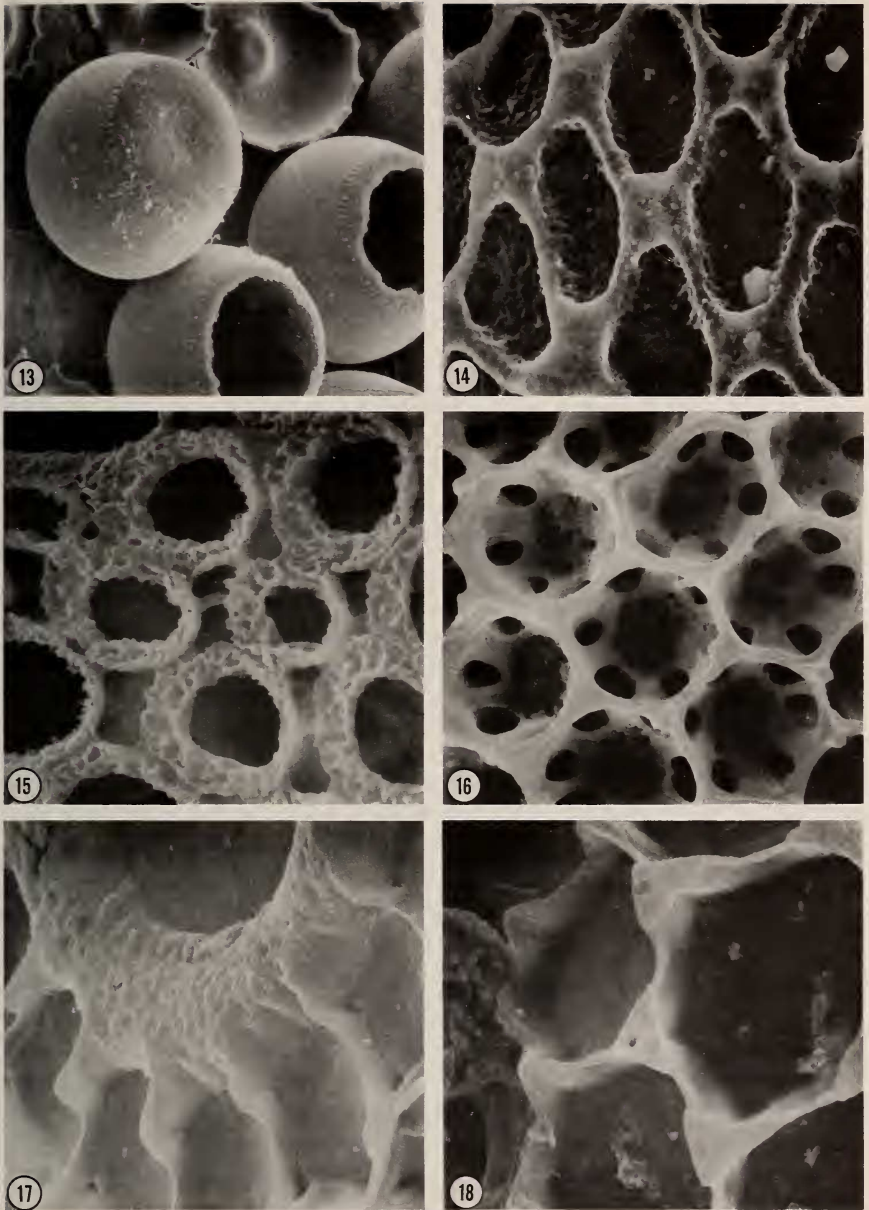
FIGS. 13–18. Eggs of Riodinidae and Lycaenidae. **13,** *Euselasia hieronymni* hatched and unhatched eggs, 60×; **14,** Porous plastron in *Brephidium pseudofea,* 600×; **15,** Rib surfaces in transition zone of *Emesis emisea,* 1800×; **16,** Inverted funnel-shaped meshwork and aeropyles in *Emesis tegula,* 360×; **17,** Flying buttress ribs near collar of *Calephelis rawsoni,* 300×; **18,** Aeropyles on rib junctures, lateral area of *C. rawsoni,* 360×. Photographs reduced to 0.58 or original size.

Emesis tegula Godman and Salvin

Figs. 5, 16, 23
d. 0.90 mm; h. 0.50 mm

Shape and external appearance much like *mandana*, only with a higher profile; cells of honeycomb reticular network shaped like inverted bowls with six large openings on lateral margins (Fig. 16) and numerous small pores on convex bottom; broad carina on ridges; thin spine or needle-like process protruding outward from each rib juncture; most of these spines are slightly recurved at their tips.

Micropyle with five holes; rosette uniquely set on an elevated hillock or pimple projecting upward from the floor of the micropylar area (Fig. 23); the elevation is so modest that this character is not visible dorsally, the specimen must be tilted slightly; petals of rosette outlined by delicate elevated ribs; micropylar surface pitted with pores which are much larger than the micropyles.

Emesis tenedia C. & R. Felder

Fig. 6
d. 0.72 mm; h. 0.40 mm

Shape and external appearance much like *mandana* and *tegula*, but generally smaller; central micropylar depression smaller (0.07 mm) and more bowl-like; transition zone between micropylar area and hexagonal cells composed of small cells whose outlining walls are relatively thick and sloping; cells on shoulder and side of the type found in *tegula*, but the central "bottom" of the pit is deeper; the large pores on the sides of the cells are often "closed," perhaps by accessory gland secretions which cover the entire egg surface during oviposition rather than just the side adhering to the plant substrate; spines projecting from the rib intersections not as long on the sides as in *mandana*, so that the dorsal view may not appear as echinoid.

Micropyle with seven or eight holes at the bottom of a gently-rounded micropylar pit; the rosette is slightly elevated above surrounding areas, though not on a hillock as in *tegula*.

Apodemia mormo mejicana (Behr)

Figs. 9, 19
d. 0.92 mm; h. 0.60 mm

Shape and profile as in *Emesis tegula*; hexagonal cells in the form of honeycomb reticulations on all visible surfaces except micropylar area; needle-like projections at rib intersections are recurved (this character may be exaggerated by artifacts induced by handling, perhaps more so in newly laid eggs); carina on ridges between spines; cells are deeply concave, cup-shaped, with open, rather large pores in lateral walls; no abrupt demarcation between rib walls and cell sides; cells adjacent to micropylar region smaller and distorted from hexagon to odd shapes tending toward the oblong; transition zone seems to be overlaid with viscous cement which on hardening, covers the ribs and cells adjacent to the micropylar region (Fig. 9) and looks artifactual.

Micropyle of five holes; rosette not distinct, seven to ten petals of a recessed type (Fig. 19); micropylar region smooth except for a suggestion of hexagon shape cells through slight depression or elevations in the surface.

Apodemia chisosensis Freeman

Figs. 10, 24
d. 0.93 mm; h. 0.48 mm

Shape and appearance much like *A. mormo*; markedly echinoid in gross view as the spiny processes at each rib intersection approach 0.04 mm length on lateral margins; ribs carinate, depressed slightly as they run between spines such that a line drawn from the tip of one spiny process to another along the surface would form a "U" shape, with the rib forming the bottom of the "U"; cells deeply inverted; large lateral pores
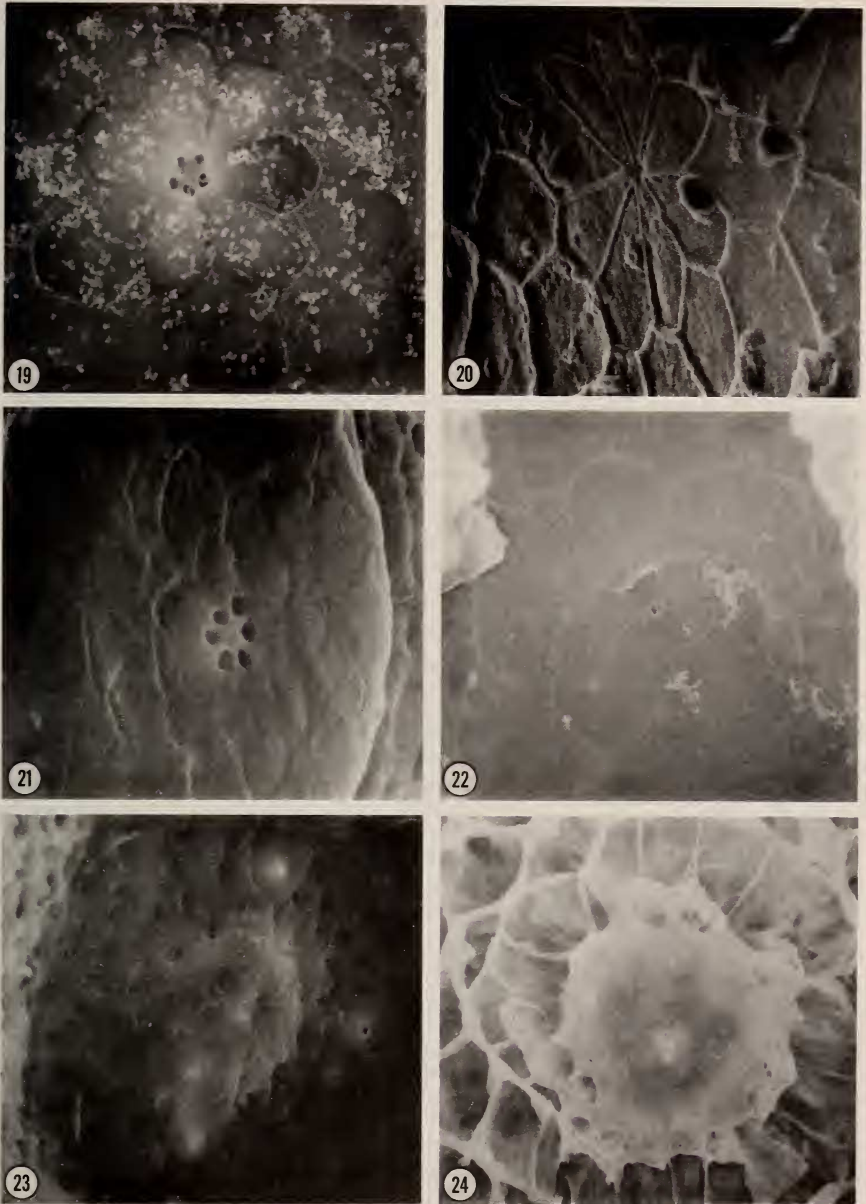
FIGS. 19–24. Micropylar regions in eggs of Riodinidae. **19,** *Apodemia mormo mejicana*; detritus on surface results from alcohol preservation, 1200×; **20,** *Lasaia sula penninsularis*, note delicate ribbing of rosette, 960×; **21,** *Emesis emisea*, depressions or troughs form rosette, 1200×; **22,** 3-hole micropyle of *Apodemia palmeri*, 1200×; **23,** *Emesis tegula* with rosette area elevated, 600×; **24,** Collar-like, lacey network surrounding micropyle in *Apodemia chisosensis*, 360×. Photographs reduced to 0.58 of original size.

almost as deep within cells as spines are high; many smaller pores in the bottom of the inverted bowl-shaped cell may serve as aeropyles.

Micropyle of 4–5 pores; four petal rosette very difficult to detect and almost obsolete; entire micropylar area and adjacent transition zone overlaid with smooth-surfaced coating which is highly porous near its margins (Fig. 24) giving it a "lacey" appearance; the elevation of the margins of this coating suggest that it was laid down after the ribs and cells were formed perhaps in an overgenerous matrix which originally delivered sperm to the micropyle.

This micropylar coating in *Apodemia mormo* and *chisosensis*, in addition to other egg characters shared by them, distinguishes them from eggs of their congeners described below.

Apodemia palmeri (Edwards)
Figs. 11, 22
d. 0.68 mm; h. 0.34 mm

Egg circular in top view, dome-shaped in profile without marked flat surface on top; micropylar area sharply depressed with transition zone having a perpendicular surface adjacent to micropylar region; ridges are broad, with thin carina at crest (becoming obsolete in spots, more apparent at rib intersections) and gradually sloping walls; cells gently depressed with six large pores on lateral margins beneath rib intersections; bottom of cells of irregular surface with many scattered small pores.

Micropyle with 3 or 4 holes; rosette present but nearly obsolete (Fig. 22).

Apodemia walkeri Godman and Salvin
Fig. 12
d. 0.72 mm; h. 0.38 mm

Shape, size and profile, as in *A. palmeri*; micropylar depression in apex of top 0.20 mm (twice as large as *palmeri*); ridges between cells rounded, with carinae, mostly limited to lateral areas where they help form stubby nipples at rib intersections; cells rather deeply concave with lateral fluting formed by up-side down tear-drop indentations separated by ribs confluent with lateral margins of ridges above (the cells resemble the die fitted by a Phillips head screwdriver); cells in transitional zone one-quarter to one-half size of more lateral cells, and of irregular to almost closed shape.

Micropyle with 4 or 5 holes; rosette not apparent in several eggs observed.

Euselasia hieronymni Godman and Salvin
Fig. 13
d. 0.50 mm; h. 0.40 mm

Egg circular from above, shaped like an upright flat topped pottery jar in profile; eggs are widest at about one-third their micropylar height from the bottom (0.12–0.13 mm) and gradually curve inward to the top shoulder. The flat top surface measures 0.36 mm, or slightly less than the height of the egg; the chorionic surface is smooth, though it may be interrupted here and there with delicate chorionic tracings resembling the silken threads left by larvae; a series of aeropyles line the lateral margins of the shoulder with a tendency for the openings to occur in pairs (Fig. 13); the aeropyles are borne on small pimple-like craters. Micropyle with three openings with a depressed area between; rosette of ten broadly joined petals of the depressed type.

Fig. 13 shows hatched as well as unhatched eggs. The larvae also consume the lateral margins of the shell, and examples of these partially eaten eggs are also on the figure. On the eaten eggs can be observed the concave inner part of the ventral surface, which conforms to that reported in *Anatole rossi* Clench, by Ross, 1965. A ventral concave surface was a predicted configuration for an "unknown" lycaenid (in Downey & Allyn, 1980).

The egg of *Hieronymni* is fairly close to being as high as wide. Only one riodinid,

the European *Nemeobius lucina* L., presently is known to us, in which the height is greater than the width (0.8 mm to 0.72 mm, according to Doring, 1955, p. 98).

Discussion

Having closely studied the chorionic architecture of these 13 species of Riodinidae, we are struck by the variability of different egg types compared to those in the larger family Lycaenidae. Indeed, there is probably as much diversity in egg pattern in these few species as in the 42 lycaenid genera treated by Clark and Dickson (1971), which included several subfamilies and tribes. A more exhaustive survey (if and when more of the relatively uncommon eggs become available) would be particularly rewarding from a taxonomic viewpoint. Too few species were examined here to warrant more than conjecture regarding inter-familial questions involving the Lycaenidae and the Riodinidae. However, we expected fewer differences than those noted, and our opinions have been influenced more in the direction of family separation than they were before.

Chorionic structures of the egg reflect the shape of the follicular epithelium in the ovarioles which secreted them and are thus the manifestation of an adult character. Whatever their significance for taxonomy, they should be correlated with that of other adult character states. What are unusual here are the marked differences among the few species examined. Had the latter been selected (they were not) on the basis of representing discrete and disparate taxonomic positions, we might not have been as impressed. We are now anxious to see samples of other riodinid eggs.

While smooth, relatively unsculptured eggs are commonly encountered in the Hesperiidae and Papilionidae, eggs with a highly sculptured chorion are the rule in the Lycaenidae and Riodinidae. The closest approach to the smooth condition so far observed, however, is in *Euselasia hironymni* where the only adornment on the relatively smooth egg consists of an inconspicuous, single ring of aeropyles around the circumference of the top lateral margin, plus a few irregular, web-like tracings almost in the nature of detritus on the surface. Even the European *Nemeobius lucina,* which tends toward the unsculptured condition, has a few scratches on the surface. *Euselasia* also has unusual oviposition behavior: eggs are laid in ordered clusters, rather than singly, as are the great majority of riodinid species so far known. This behavior could be correlated in an evolutionary sense with the lack of egg sculpturing. Most of the species have highly ornamented eggs with ridges, tubercles, crests and spiny elevations, easily observed with a low power hand lens.

The eggs of some congeners show sufficient diversity to suggest

further taxonomic study. The egg of *Emesia emisea* for example, is clearly distinct from those of *E. mandana, tegula* and *tenedia. Apodemia mormo* and *A. chisosensis* also are clearly related, but distinct, when compared to eggs of *A. palmeri* and *A. walkeri.*

We are struck by the lack of plastrons in the Riodinidae, since such structures are common in the Lycaenidae (Fig. 14). Most lycaenid eggs (particularly in the Theclinae, Lycaeninae, Polyommatinae and Miletinae) have much of the subsurface chorion (beneath the reticular network of ridges and tubercles) perforated by many small pores which enable the highly porous chorion to serve as an air store and plastronic network. This thin-film air mass serves as a physical gill when submerged in rain water, which is rich in dissolved oxygen. The small pores of the plastron type were only noted in *Apodemia chisosensis*, though the micropylar regions of *Emesis* species (other than *emesia*) contain pores. In the latter species we suspect micropylar respiration, particularly because of the lack of aeropyles, and pores of any other sort. Aeropyles were found in *Apodemia, Lasaia, Caria* and *Calephelis*, but the size and number of these openings was no greater than the same structures in lycaenid egg types, even though the lycaenids also are equipped with the plastronic pores.

While lacking plastrons (in general), some riodinid eggs are highly suggestive of lycaenid types. For example, *Apodemia mormo* and *A. chisosensis* resemble the eggs of temperate lycaenids, but others in the same genus (*walkeri, palmeri*) are much further removed in facies from a lycaenid type. Interestingly, there is some evidence of Nearctic speciation in both *Apodemia* and *Calephelis*, and perhaps the resemblance of egg types in some members of the former genus to lycaenid types has been attained through ecotypic convergence. *Calephelis*, however, is morphologically far removed from the lycaenid condition, whose closest approach to the hexagonal eggs would be found only in the Oriental Poritinae.

We are making some attempt to relate egg structure with adaptive strategies, but beyond such generalities as might be indicated by plastronic respiration, we have not as yet found any major differences in egg-laying strategies which correlate with these different egg structures.

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